

CHANGES IN LIFE ORIENTATION DURING THE ONTOGENY OF SOME HETEROMORPH AMMONOIDS

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ABSTRACT. To understand the mode of life of *Eubostriochoceras muramotoi* Matsumoto, 1967, and some other heteromorph ammonoids from the Upper Cretaceous of Hokkaido, Japan, their life orientation and growth patterns were restored using a hydrostatic model and differential geometry. The adequacy of these restorations was tested using the obliquity of ribs and its change during ontogeny. Rib obliquity parallels the aperture at every growth stage and corresponds well to the inferred changes of life orientation. The pattern of rib obliquity was also deduced from a computer simulation, programmed so that growth occurs only at the aperture which keeps a constant angle to the sea floor. In most heteromorphs, the computer-produced profiles approximate well to actual rib patterns. Although the rib obliquity of these ammonoids may appear to change somewhat capriciously, it must be functionally regulated. Except during the early orthoconic stage of growth, a floating or lightly touching benthonic mode of life is strongly suggested.

THE ammonoid shell is composed of a phragmocone and a living chamber. During life, the average density of a living chamber filled with soft parts was greater than that of sea water, while the phragmocone was buoyant due to the gas it contained. If an ammonoid could float like extant *Nautilus*, the average density of the whole animal must have been approximately equal to the density of sea water. On this basis, Trueman (1941) estimated the buoyancy potential of some ammonoids; similar assumptions were made in the estimation of total average densities of various ammonoids by Reymont (1958, 1973), Heptonstall (1970), Tanabe (1975, 1977), and Ward and Westermann (1977).

This type of hydrostatic model enables further inferences to be made about life orientation. When an ammonoid floated in sea water, buoyancy and gravity must have balanced and their respective centres must have lain on a vertical line. So if these centres are estimated in an actual ammonoid, its life orientation can be determined. Trueman (1941) first illustrated such living attitudes in both normally coiled and heteromorph ammonoids. Further developing this theory, Raup (1967) and Saunders and Shapiro (1986) restored the life orientation of some normally coiled ammonoids and discussed their functional morphology. However, the change of life orientation during the ontogeny of heteromorph ammonoids has been little studied (probably because their complicated coiling was difficult to model).

Okamoto (1988) recently proposed a 'growing tube model' to reconstruct the three-dimensional coiling of heteromorph ammonoids. This model involves a modification of the Frenet frame (moving frame), an established method of differential geometry and useful for the analysis and description of any regular space curve. Computer simulations which combine Trueman's concept and the growing tube model can aid our understanding of the life orientations of heteromorph ammonoids.

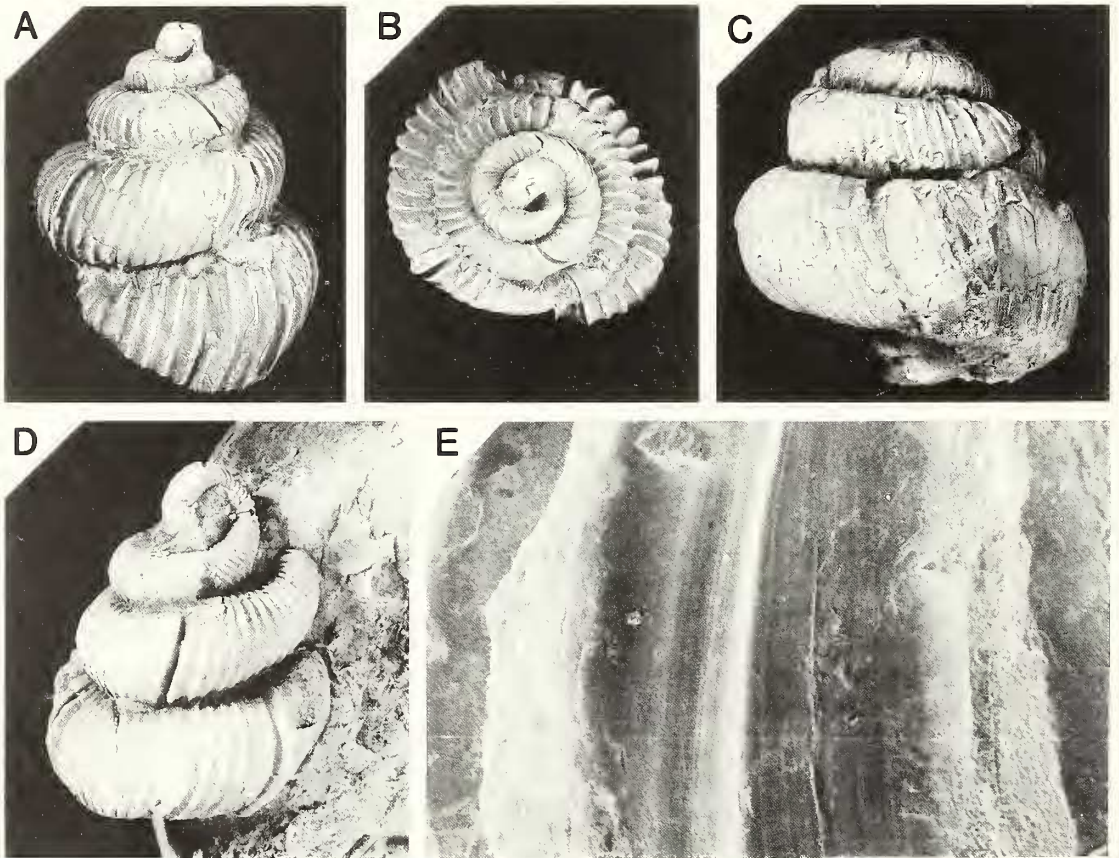
Previous discussions of buoyancy and life orientation seem to have depended on speculative calculations, and the results have not been tested using independent evidence. The complicated but regular coiling patterns of most heteromorph ammonoids reveal more about life orientation and its change during ontogeny than planispiral cephalopods.

MATERIAL AND METHODS

Abundant, well-preserved heteromorph ammonoids occur in the Upper Cretaceous of Hokkaido, Japan, with certain nostoceratids being particularly known for their curious mode of coiling. The coiling geometry and life orientation of several such species of Nostoceratidae are discussed below, especially that of the Coniacian *Eubostrychoceras muramotoi* Matsumoto, 1967. The repositories of the specimens examined are: UMUT, University Museum, University of Tokyo; GK, Department of Geology, Kyushu University; WEA, Institute of Earth Science, Waseda University; KPMG, Kanagawa Prefectural Museum.

Eight specimens of *E. muramotoi* from the Obira area, Hokkaido, were available. The study of these and other previously described specimens reveals the following characters:

1. *Coiling pattern.* Matsumoto (1967) described the coiling pattern of the holotype (GK.H5589; text-fig. 1D) as follows: 'The earliest shell is nearly straight, ascending and then followed by a subcircularly curved half whorl, which in turn is twisted obliquely down, passing to the main helical whorls, whose axis of coiling is along the earliest straight shaft'. The same mode of coiling is apparent in another nearly complete specimen (WEA 003T-1), where although the earliest stage is concealed by later helicoid whorls, the direction of the orthoconic shaft is inferred to be the coiling axis of the whorls (text-fig. 1A, B). In this sample, six specimens are dextrally coiled like the holotype (text-fig. 1D) and two are sinistrally coiled (text-fig. 1C).



TEXT-FIG. 1. *Eubostrychoceras muramotoi* Matsumoto. A, WEA 003T-1, from Obirashibe River (near mouth of Okufutamata-zawa tributary), Obira area; Coniacian; lateral view, $\times 1.5$. B, apical view of the same specimen, $\times 1.5$. C, WEA 004T, from the same locality; lateral view of sinistral specimen, $\times 1$. D, GK.H5589 from Pombetsu, Go-no-sawa, Ikushumbetsu area; Coniacian; upper view of holotype, $\times 2$. E, WEA 003T-2, from the same locality as specimen in A; SEM photograph indicating conformable relation between ribs and growth lines, $\times 25$.

2. *Change of rib obliquity.* Oblique and gently flexuous ribs are regularly developed on the whorls. In the helicoid stage, there are about forty ribs per whorl. Matsumoto (1967) noted that a drastic change of rib obliquity occurs in the middle growth stage, one and a half or two whorls after the shell's turning-point. The change occurs in every specimen studied (text-fig. 1A, C).

3. *Growth lines.* Fine striae occur between the ribs (text-fig. 1E). They run parallel to the ribs at every stage, and appear to be growth increments. The rib obliquity, therefore, seems to indicate the shape of the aperture at each growth stage.

4. *Living chamber.* The length of the living chamber in WEA 003T-1 appears to occupy about one and a quarter whorls of the helicoid stage. The length of the living chamber may be 40-50% of the total cone length, but because it is always more or less deformed or damaged, the precise estimation of this ratio is difficult.

5. *Whorl cross-section.* The shape of the whorl cross-section is almost circular. Shell thickness is about 2% of whorl radius; this value is very small, but the shell seems to be reinforced by sharp ribs which occur regularly on the whorls.

COILING GEOMETRY

Expression of coiling form

Raup (1966) proposed a generalized growth model to express the shell form of most gastropods, cephalopods, and bivalves. Heteromorph coiling forms, however, cannot be described completely by his model. Okamoto (1984) succeeded in modelling *Nipponites* (a Cretaceous heteromorph ammonoid) by regarding the shell as a meandering tube with circular cross-section. In this model, the locus of the tube's centre \mathbf{R} and the corresponding tube radius r define a tubular body: the tube's surface is expressed by $\mathbf{U} = \mathbf{R} + r$ and $r \cdot \dot{\mathbf{R}} = 0$, where $\dot{\mathbf{R}}$ is the differential of \mathbf{R} and indicates the growth direction of the tube.

Because normal cross-sections of the shell of *E. muramotoi* can also be treated as circles, it can be modelled similarly. In its early growth the shell of *E. muramotoi* approximates to an orthoconic tube. After a sharp bend, the shell coils helically around the earlier orthoconic shaft, and the whorls become almost isometrically helicoid. Consider now a cylindrical coordinate system in which the locus of the tube's centre line is expressed by a parameter i . The direction of increase of i is the tube's growth direction. Its projection on the $X-Y$ plane, which is perpendicular to the coiling axis, is approximately an equiangular spiral (text-fig. 1B). If D is the distance between the coiling axis and the tube's centre line, D increases simply with growth i and may be expressed as an exponential function of i :

$$D = 10^{ai + a_0}$$

where a and a_0 represent the whorl expansion rate and its initial value of D respectively. If Z represents the displacement of the tube's centre line along the coiling axis, the tube's centre at every stage sits on one particular hyperbola (text-fig. 2A) and its trace follows this hyperbola's revolution around an asymptotic line (text-fig. 2B). When the two asymptotic lines of the hyperbola are expressed as $D = 0$ (coiling axis) and $Z = -bD$, Z is expressed as a function of D :

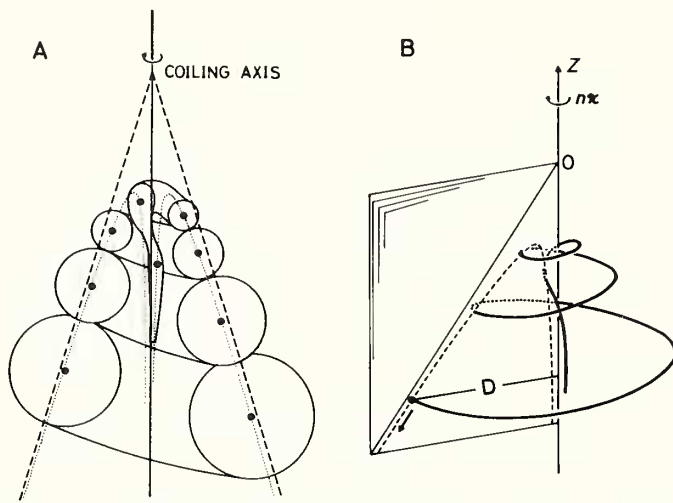
$$Z = -bD + \frac{d}{D}$$

where the coefficient b is related to the apical angle of the specimen, and the coefficient d expresses the 'pointedness' near the whorl's turning-point. If the revolution angle is $n\pi$, the angular velocity $\Delta n/\Delta i$ is not constant: it is almost zero in the earliest orthoconic stage but maintains a constant value in the later helicoid stage. Therefore, the relationship between n and i can also be expressed as a hyperbola:

$$i = n - \frac{1}{n} - f \quad (n > 0)$$

where the coefficient f indicates the coordinates of i where the two asymptotic lines ($i = 0$, $i = n - f$) intersect together. Finally, the whorl radius r is defined as a function of the length l of the tube centre line. If the radius increases isometrically relative to whorl length, then $2r = cl$, where coefficient c is the relative growth ratio of tube diameter to tube length.

Therefore, four equations are required to express the shape of *E. muramotoi*, with six coefficients: a , a_0 , b , c , d , and f . The values of a (whorl expansion rate), b (apical angle), and c (radius enlarging rate) were obtained directly (from WEA 003T-1), but the relationship between the other coefficients and shell shape is not so obvious. Approximate values of these latter coefficients were estimated empirically so as to fit the model most closely to the actual coiling pattern. The following values for the six coefficients of the hyperbolic model were determined: $a = 0.075$, $a_0 = 1.4$, $b = 2.97$, $c = 0.051$, $d = 4$, and $f = 2$. This model can be applied to other heteromorph ammonoids, such as *Muramotoceras yezoense* Matsumoto and *Ainoceras kamuy* Matsumoto and Kanie; and, although not suitable for growth simulation, it is useful for the description of their shell form.



TEXT-FIG. 2. *Eubostrychoceras muramotoi* Matsumoto; coiling pattern and its model. A, hypothetical whorl cross-section. B, revolving hyperbola model, indicating the whorl centre line.

Analysis of growth

Okamoto (1988) proposed a 'growing tube model' for analysing the growth pattern of any coiled shell. In this model, a coiled shell with circular whorl section can be generally described by three differential parameters (op. cit., text-fig. 7): E , radius enlarging rate; C , standardized curvature; and T , standardized torsion. Each parameter changes with a growth stage parameter s . Using this method, any heteromorph ammonoid can be uniquely described on a plane diagram involving the three functions of growth stage, $E(s)$, $C(s)$, and $T(s)$.

In practice, E , C , and T for *E. muramotoi* can be calculated by invoking the hyperbolic model described above, but modified in two ways to make it correspond more closely to real specimens (Okamoto 1988): 1, a higher E value is estimated for the earlier growth stage; and 2, C is controlled so as not to exceed the theoretical limit ($C = 1$) throughout the growth. The growth pattern of this species can be divided into two stable stages (orthoconic and helicoid) with an intervening transitional interval (the turning-point). The sudden change of coiling mode at this transitional interval may indicate a change in mode of life.

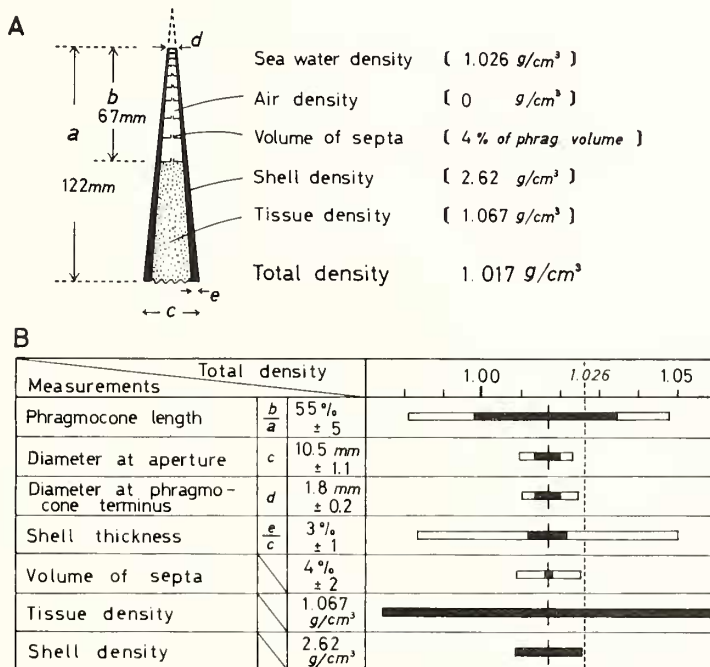
LIVING ATTITUDE

Estimation of buoyancy potential

If the particular growth pattern ($E(s)$, $C(s)$, $T(s)$) for a specimen is given, various physical characters (e.g. tube length, surface area, volume, centre of gravity, etc.) can be calculated from the growing tube model. Trueman (1941) argued for the potential buoyancy of some ammonoids by estimating the volume and density of phragmocone and living chamber. Raup and Chamberlain (1967) and Heptonstall (1970) also referred to the estimation of buoyancy potential. Tanabe (1975, 1977) and Ward and Westermann (1977) applied a similar method to the buoyancy potential of heteromorph ammonoids and discussed their functional morphology.

Here I evaluate the adequacy of current methods for the estimation of ammonoid buoyancy. To estimate the total density of *E. muramotoi*, several density values are assumed (text-fig. 3A) for a simplified conical shell form. I adopt the densities of shell and soft parts estimated by Reyment (1958) and Denton and Gilpin-Brown (1966) using living *Nautilus*. Secondly, the following five values were measured or estimated from the actual specimen or its growing tube model: the ratio of phragmocone length to total cone length; diameter of aperture; whorl diameter at the phragmocone's termination; shell thickness; and volume of septa. (Though shell thickness is taken to be *c.* 2% of whorl radius, a somewhat higher value may be appropriate, because the volume of ribs should be taken into consideration.) The calculation gives a total density for this specimen of 1.017, which is less than that of sea water, 1.026 (text-fig. 3A).

However, the calculated total density is quite unreliable because it may be seriously influenced by



TEXT-FIG. 3. Calculation and error estimation of total density of *Eubostyrioceras muramotoi* Matsumoto, WEA 003T-1. A, estimated physical values. B, estimated error range for each value. Black rectangles show the fluctuation range of total average density when each value is 5% over- or underestimated. White rectangles show the fluctuation range as estimated from each measuring error.

slight errors in each estimated value. The confidence interval of the calculated total density is shown in text-fig. 3B. Black rectangles show the fluctuation range of total average density when each value is 5% over- or underestimated. Some error bars extend beyond the critical line of 1.026. While the value assumed for tissue density is unlikely to be as much as 5% incorrect, that of the ratio of phragmocone length to total cone length and shell thickness cannot be estimated to within a 5% margin of error. If a multiplication of these errors occurs, the confidence interval of calculated total average density must increase seriously. It is almost impossible to discuss sensibly the buoyancy regulatory ability of *E. muramotoi* from the result of this calculation.

Life orientation

Hydrostatic models for the life orientation of floating ammonoids were discussed by Trueman (1941), Raup (1967), Raup and Chamberlain (1967), and Saunders and Shapiro (1986). Trueman (1941) intuitively estimated the life orientation of some heteromorph ammonoids from the relationship between buoyancy and gravity. Klinger (1981) divided some heteromorph ammonoids into four groups, and discussed their mode of life from the standpoint of possible buoyancy control. Ebel (1985) argued that the hydrostatics of some ammonoids favoured a gastropod-like mode of life. However, little is known of the life orientation of heteromorph ammonoids from a hydrostatic standpoint. This is probably because no geometrical model had been devised which was capable of accurately describing heteromorph forms. Application of the growing tube model enables various physical properties to be calculated easily by microcomputer. Reconstructions of the life orientation of ammonoids based on this model require three assumptions to be made:

- 1, the floating position during life can be restored by assuming that the buoyancy of the phragmocone was just balanced by the weight of the living chamber in sea water.
- 2, for simplicity, the phragmocone and living chamber of ammonoids are regarded as being composed of homogeneous materials.
- 3, the ratio of phragmocone length to living chamber length was constant throughout growth; there is no certainty that the ratio was invariable in actual specimens, but the assumption is reasonable as a first approximation because the same total density was maintained at every growth stage if shell radius increased isometrically with shell length.

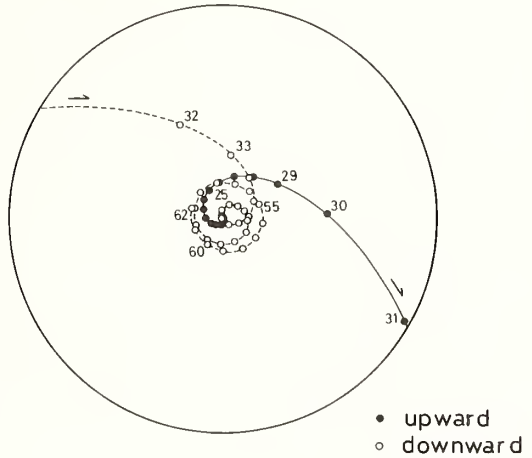
If the centre of gravity of the phragmocone G_1 , and that of living chamber G_2 are calculated at a given growth stage, the vector from G_1 to G_2 must be directed vertically. The centres of gravity can be determined in the following way. First, the cone is separated into many 'slices' by considering normal cross-sections parallel to the generating curve. The centre of gravity of each slice must be situated at the distance $Cr/4$ away from the slice centre in a direction towards the maximum growth point of the whorl surface, where C and r are the standardized curvature and the radius of the generating curve, respectively. The centres of gravity for the phragmocone and the living chamber are separately determined by integrations of the volume and the centre of gravity about each slice. If the centre of gravity of each slice and its volume are given by (g_x, g_y, g_z) and V , respectively, the centres of gravity for the two parts can be calculated as follows:

$$G(x, y, z) = \left(\frac{\sum g_x V}{\sum V}, \frac{\sum g_y V}{\sum V}, \frac{\sum g_z V}{\sum V} \right)$$

In practice, both centres of gravity can be estimated by microcomputer through integration of numerous slices, each $r/10$ in length.

Phragmocones and living chambers of real ammonoids were not, in fact, homogeneous: heavier shell formed the 'outside' while the 'inside' was filled with lighter materials, such as air, cameral liquid, and soft parts. Consider the extreme example of a hollow cone in which the mass is concentrated on its surface. In this case, the centre of gravity of the slice must be situated at a point $Cr/2$ away from the slice centre, towards the maximum growth point on the surface; the centre of gravity shifts $Cr/4$ further

from its position when the shell is assumed to be homogeneous. Estimation of the vertical direction becomes somewhat more complicated, requiring knowledge of both the centre of gravity of the total mass and the centre of buoyancy. The former cannot be calculated without making assumptions about density. However, since the difference in results between the two methods is small enough not to seriously influence the vertical vector, the phragmocone and living chamber are both regarded here as effectively homogeneous.



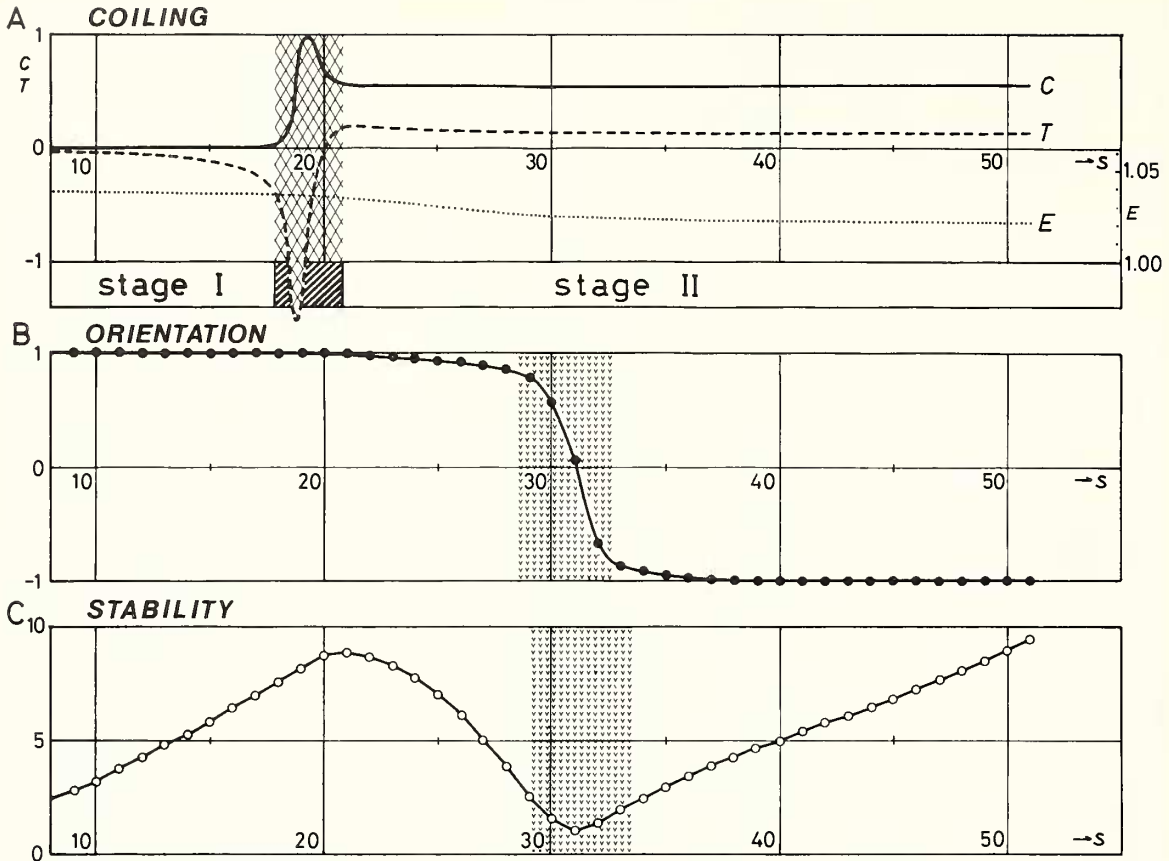
TEXT-FIG. 4. Stereographic projection on Wolff's net (lower hemisphere) showing ontogenetic change of the vertical vector relative to the coiling axis for *Eubostrychoceras muramotoi* Matsumoto. Vertical vector is defined as direction from centre of buoyancy to centre of gravity; coiling axis is fixed at centre of diagram.

The great merit of this method is that life orientation can be restored without making questionable assumptions concerning shell thickness and density of soft parts. In this hydrostatic model, only the growth pattern of the shell and one constant (ratio of phragmocone length to total cone length) are necessary. For *E. muramotoi* the former is estimated by moving frame analysis (text-fig. 5A; Okamoto 1988) and the latter measured at about 0.55 from a real specimen. From such data, the direction and magnitude of the vertical vector can be calculated at various growth stages. The change of direction of the vertical vector during ontogeny can be projected on a Wolff's net (text-fig. 4). As the result of this simulation, the direction of the vertical vector is seen to turn over abruptly at stages 30–32. The magnitude of the vertical vector represents a kind of 'stability index', because it measures distance between the two centres of gravity. Although this value generally increased with growth, it reached a minimum when the living attitude flipped over.

RESULTS OF SIMULATIONS

Simulation of Eubostrychoceras muramotoi

In *E. muramotoi*, both the growth pattern obtained from moving frame analysis and the results of simulating life orientation are shown in text-fig. 5. There is a transitional interval in the growth pattern when the mode of coiling changes drastically, seemingly indicating a change in mode of life. The Z (coiling axis) component of gravitational force, standardized with a unit vector, is shown in text-fig. 5B. The rapid turnover of living attitude (stages 30–32) occurs after the initiation of helical coiling (stage 19). At turnover, the magnitude of the vertical vector is minimized (text-fig. 5C), and the living attitude may be unstable. Using the result of text-fig. 4, theoretical life orientations can be reconstructed for several growth stages by computer graphics (text-fig. 6). The turnover of life orientation occurs one and a half or two whorls after the turning-point in shell growth. Interestingly, though the mode of coiling does not change, an abrupt change in rib obliquity occurs just at this stage in real specimens (text-fig. 1).



TEXT-FIG. 5. Diagrammatic figures showing change of some geometric and physical values during ontogeny of *Eubostriyoceras muramotoi* Matsumoto. A, moving frame analysis. B, Z component of unit vertical vector. C, length of vertical vector, a kind of stability index (see text).

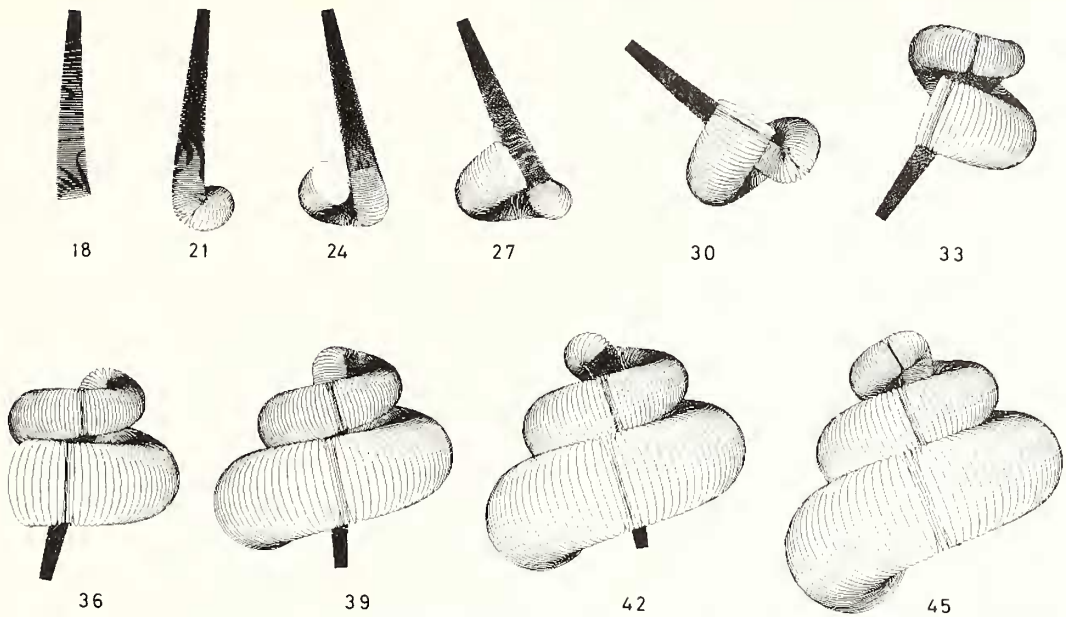
Simulation of other heteromorph ammonoids

Okamoto (1988) also described the coiling patterns of several other heteromorph species by moving frame analysis, and the changes in their life orientation during ontogeny can be simulated by the same method.

1. *Ainoceras kamuy* Matsumoto and Kanie, 1967. The coiling pattern of *A. kamuy* in its early-middle growth stage resembles that of *E. muramotoi* (text-fig. 7A, B), and a similar change of life orientation is suggested (text-fig. 8A). Moreover, an analogous change of rib obliquity occurs at the corresponding stage (text-fig. 7B). After its helical coiling phase, this species goes through another significant change of coiling pattern, forming a loose and nearly planispiral whorl in later life. Life orientation also appears to change at the beginning of this last stage (text-fig. 8A), and it is interesting to note that rib obliquity changes from prorsiradiate to rectiradiate at this point.

2. *M. yezoense* Matsumoto, 1977. This species (text-fig. 7C) also has a similar coiling pattern to *E. muramotoi*. However, the loosely coiled helicoid shell, with its larger apical angle, suggests a more gradual and incomplete turnover of life orientation (text-fig. 8B). Rib obliquity also changes gradually at the corresponding growth stage (text-fig. 7C).

3. *E. japonicum* (Yabe, 1904). This species shows a different coiling pattern from the foregoing species. The shell exhibits crioceratoid coiling in early growth, then forms an open helicoid spiral



TEXT-FIG. 6. Computer graphics showing inferred change of life orientation during ontogeny of *Eubostrychoceras muramotoi* Matsumoto. The turnover of life orientation occurs at one and a half or two whorls after the shell's turning-point.

(torticone) in its middle stages (text-fig. 7D). Presumably some change of life orientation occurred between the two stages; rib orientation also changes from rectiradiate to prorsiradiate (text-fig. 8C).

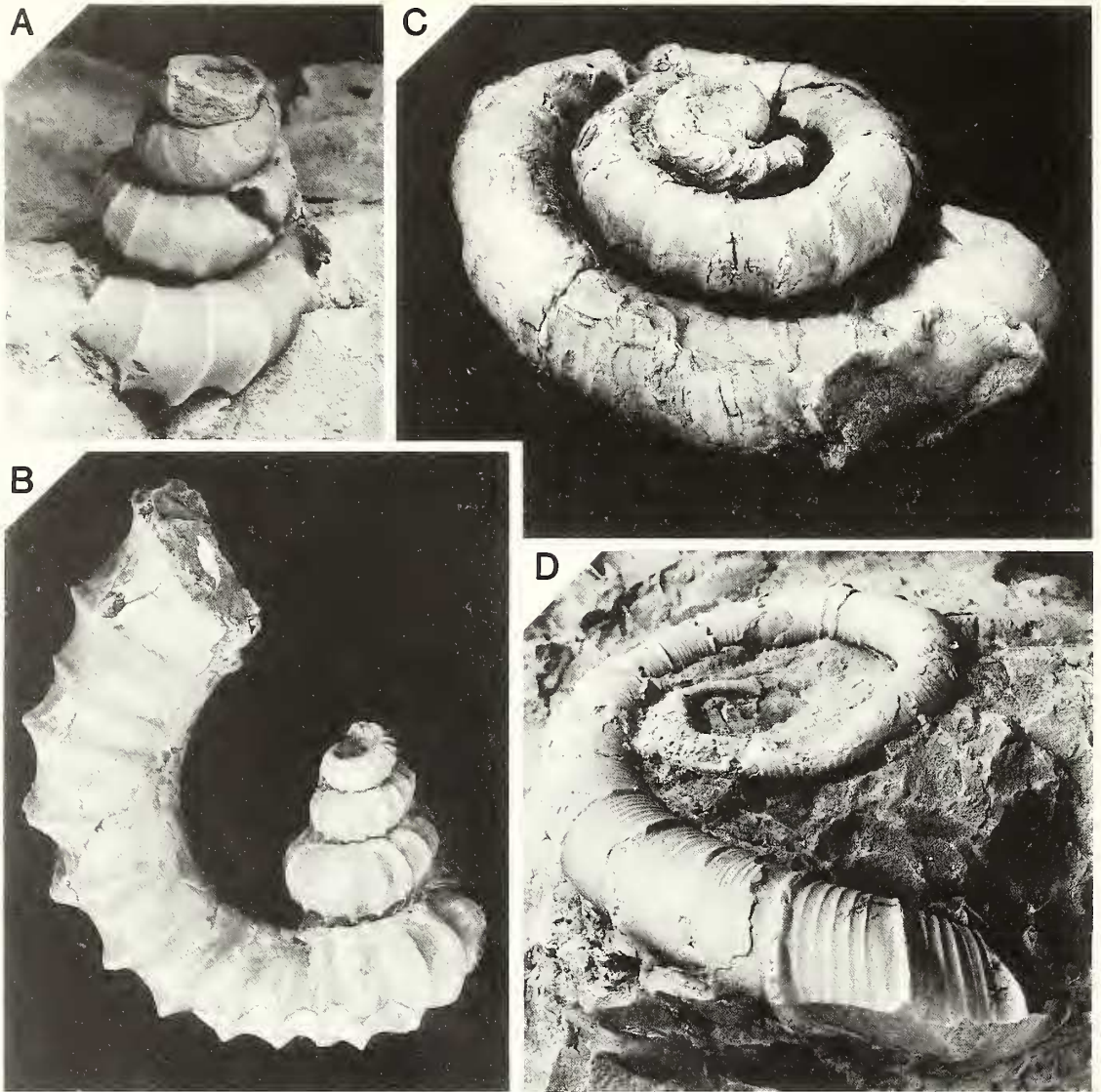
Rib obliquity seems to be influenced by life orientation. As stated above, the growth lines of *E. muramotoi* run parallel to the ribs, and rib obliquity indicates the shape of the aperture at every growth stage. This is also the case in other heteromorph species. It is supposed, as a working hypothesis, that these floating ammonoids grew oblique apertures to maintain a constant angle with the vertical vector.

FURTHER OPERATIONS

Simulation of rib obliquity

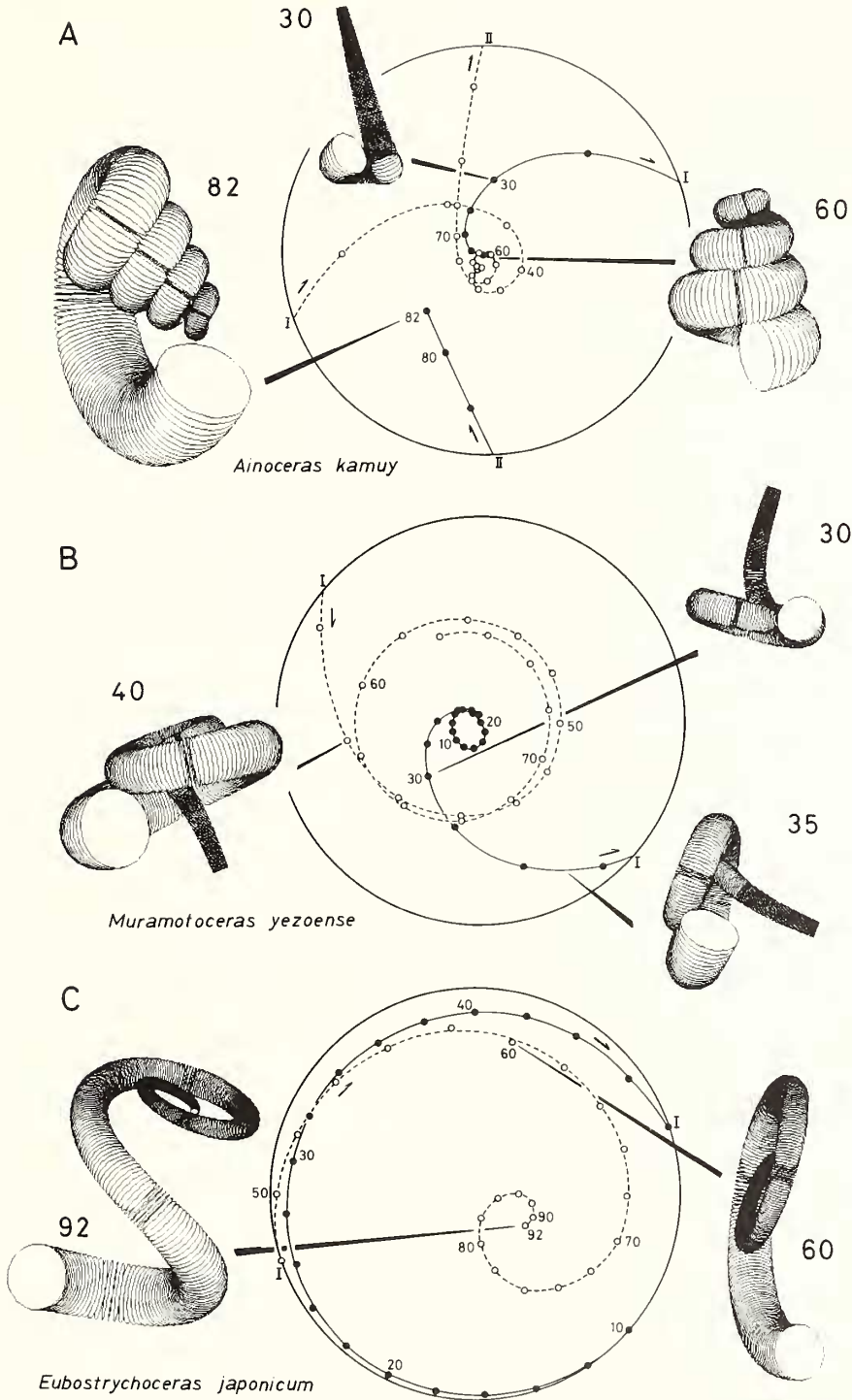
On the basis of the above working hypothesis, a theoretical rib pattern can be simulated from the estimated life orientation. Rib shape and obliquity can be determined as follows (see also text-fig. 9). First, the 'bottom margin' and 'top margin' are defined on the generating curve of the growing tube model. When the growing tube model is oriented in life position, the bottom margin indicates the lowest point on the generating curve, and the top margin indicates the opposite point to it. The generating curve is then transformed into the 'aperture curve', which is generally elliptical in shape. In this transformation, each point on the generating curve moves in a progressive or regressive direction, and the point on the bottom margin or top margin shifts the furthest. By this procedure the apertural plane is determined at every growth stage, so as to keep a constant angle to the vertical vector. Text-fig. 10A shows a computer-produced profile of the rib pattern of *E. muramotoi* with the aperture angle set at 40° (determined from a real specimen, at the last whorl in this case).

The theoretically produced profile of *E. muramotoi* is quite similar to the real specimen, in both its general outline and the abrupt change of rib obliquity in the early helicoid stage. The patterns of rib obliquity of the three other nostoceratids studied were simulated by the same method (text-fig.

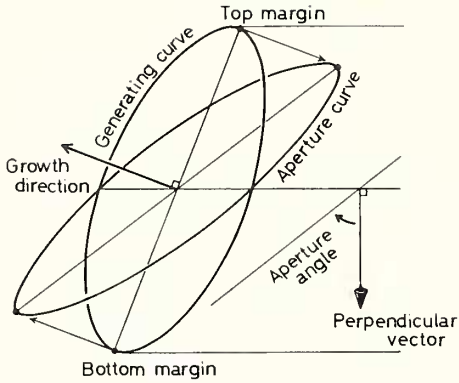


TEXT-FIG. 7. Nostoceratids from central Hokkaido, Japan, showing characteristic change of rib obliquity. A, *Ainoceras kamuy* Matsumoto and Kanie, UMUT MM17972, from the southern tributary of Rubeshibe-zawa, Saku area; Campanian; early growth stage, $\times 8$. B, same species, GK.H5577, from the third tributary of the Nio-no-sawa, Saku area; Campanian, $\times 3$. C, *Muramotoceras yezoense* Matsumoto, WEA 001Y, from Pankemoyuparozawa, Oyubari area; Turonian, $\times 1.5$. D, *Eubostrychoceras japonicum* (Yabe), KPMG 6373, from upper stream of Kotambetsu River, Kotambetsu area; Turonian, $\times 2$.

10B, C, D). Each theoretical profile is sufficiently similar to the actual rib pattern for the hypothesis about the relationship between life orientation and rib obliquity to be generally accepted. So although the rib pattern of some nostoceratid ammonoids may appear to change somewhat capriciously, it is functionally regulated. In ordinary planispiral ammonoids, constant life orientation is supposed throughout growth because they maintained a geometrically similar shell form. Theoretical rib obliquity must also be constant; in fact, specimens of many normally coiled ammonoids exhibit an



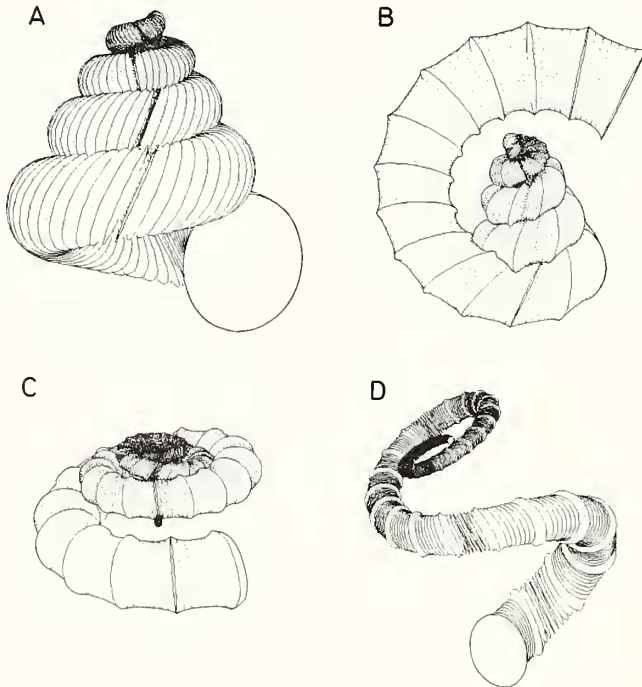
TEXT-FIG. 8. Stereographic projections on Wolff's net showing the change of vertical vector relative to coiling axis during ontogeny; computer graphics show life orientation at each growth stage. A. *Ainoceras kamuy* Matsumoto and Kanie. B. *Muramotoceras yezoense* Matsumoto. C. *Eubostriyoceras japonicum* (Yabe). The phragmocone length/total cone length ratio in these three species is taken as 0.6, 0.5, and 0.7 respectively.



TEXT-FIG. 9. Transformation of generating curve of growing tube model to 'aperture curve'. Each point on the generating curve moves in a progressive or regressive direction, so as to maintain a constant aperture angle.

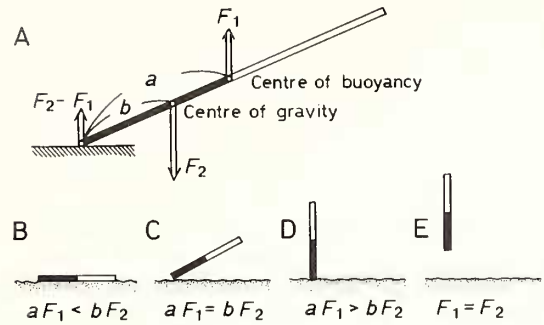
almost constant rib obliquity. This is compatible with the hypothesis of constant apertural angle, but the presumed life orientation is hardly testable in this case.

However, it is uncertain whether or not such regularity is always maintained by heteromorph ammonoids. For example, rib obliquity in the orthoconic early stage of *E. muramotoi* cannot be explained by this model. The rib pattern of *Polyptychoceras* sp., which is prorsiradiate in the early orthoconic stage and nearly rectiradiate after the first U-turn, is also difficult to simulate. If actual rib obliquity does not conform to the theoretical rib pattern, one or more assumptions in the model may be wrong. Two possible interpretations are: 1, the estimation of life orientation is inadequate because the real mode of life was quite different (e.g. purely benthonic); or 2, the aperture does not always maintain a constant angle to the vertical vector. These exceptional cases are important for our understanding of the general mode of life of heteromorph ammonoids, and require further study.



TEXT-FIG. 10. Computer-graphics showing the theoretical rib obliquity with constant aperture angle. A, *Eubostrychoceras muramotoi* Matsumoto. B, *Ainoceras kamuy* Matsumoto and Kanie. C, *Muramotoceras yezoense* Matsumoto. D, *E. japonicum* (Yabe). The aperture angles of these species are set at 40°, 60°, 40°, and 40° respectively.

TEXT-FIG. 11. Possible life orientations of the simple orthoconic model. When buoyancy F_1 , gravity F_2 , distance between the contact point and centre of buoyancy a , and distance between the contact point and centre of gravity b are given as in A, the three possible attitudes are determined by the interaction of two moments, as shown in B-D. E shows floating attitude.



Sinking attitude

I have failed to obtain any direct evidence for a floating mode of life in nostoceratid ammonoids from the calculation of total density. However, reconstruction of a life orientation which cross-checks with observations of actual rib patterns is significant. But does this result really *prove* that heteromorph ammonoids floated during life? Let us examine whether a benthonic mode of life was possible.

For simplicity, consider the sinking attitude of an orthoconic ammonoid (text-fig. 11A), where the centre of buoyancy, centre of gravity, and contact point on the bottom must lie along a straight line. When buoyancy F_1 , weight F_2 , distance between contact point and centre of buoyancy a , and distance between contact point and centre of gravity b are given, the final attitude is determined by the interaction of two moments aF_1 and bF_2 . Three attitudes are possible: 1, if the load acting on the contact point is sufficiently large ($aF_1 < bF_2$), the shell lies down on the bottom; 2, if the load is below the limit ($aF_1 > bF_2$), the shell shows an upright posture equivalent to the floating state; or 3, if the two moments balance each other ($aF_1 = bF_2$), the shell assumes an oblique posture which is quite unstable (text-fig. 11).

Generally, the sinking posture of an ammonoid shell is determined by the relationship between the centre of buoyancy, centre of gravity, contact point, and forces acting on these points. Actually an oblique posture may be possible when these three points are not situated on a straight line. But, if the load acting on the contact point were sufficiently small, the shell would take almost the same orientation as when floating. Therefore, even though the changing pattern of rib obliquity is satisfactorily explained by a floating mode of life, it is not necessarily *proved*; text-fig. 11D, E show the two possible life orientations for the main growth stages of those heteromorph ammonoids studied here.

SUMMARY AND CONCLUSIONS

This investigation of theoretically and hydrostatically possible life orientations for several nostoceratid ammonoids has shown that:

- 1, their shell form can be described by a revolving hyperbolic model.
- 2, by moving frame analysis, the growth pattern of *E. muramotoi* is separable into two stable stages, with a transitional interval indicating some change in mode of life.
- 3, the calculation of total density of ammonoids inevitably involves considerable error, and traditional methods involving speculative densities for various portions should not be used to estimate the buoyancy of heteromorph ammonoids.
- 4, changes of life orientation during ontogeny can be estimated by computer simulation, with a hydrostatic model; the turnover of life orientation corresponds well to the change of rib obliquity on real specimens of *E. muramotoi* and the three other heteromorph ammonoids studied.
- 5, these nostoceratids either floated freely or lightly touched the sea bottom.
- 6, nostoceratids with such a mode of life seem to have maintained their apertures at a constant angle to the vertical vector.

It is important to emphasize that the adequacy of this hydrostatic model was tested independently, i.e. by the change of rib obliquity during ontogeny. A constancy of apertural angle to the vertical was probably also maintained by ordinary planispiral ammonoids, but any resulting inference concerning their life position suffers from circular reasoning. The three-dimensional and complicated morphology of heteromorph ammonoids promises to be a rich source of enquiry for the solution of various general problems of functional morphology in ectocochlian chambered cephalopods.

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REFERENCES

- DENTON, E. F. and GILPIN-BROWN, J. B. 1966. On the buoyancy of the pearly *Nautilus*. *J. mar. biol. Ass. U.K.* **46**, 723–759.
- EBEL, K. 1985. Gehäusespirale und Septenform bei Ammoniten unter der Annahme vagil benthischer Lebensweise. *Paläont. Z.* **59**, 109–123.
- HEPTONSTALL, W. 1970. Buoyancy control in ammonoids. *Lethaia*, **3**, 317–328.
- KLINGER, H. C. 1981. Speculations on buoyancy control and ecology in some heteromorph ammonites. Pp. 337–355. In HOUSE, M. R. and SENIOR, J. R. (eds.). *The ammonoidea. Spec. Vol. Syst. Ass.* **18**, 593 pp.
- MATSUMOTO, T. 1967. Evolution of the Nostoceratidae (Cretaceous heteromorph ammonoids). *Mem. Fac. Sci. Kyushu Univ. Ser. D, Geol.* **18**, 331–347, pls. 18 and 19.
- 1977. Some heteromorph ammonites from the Cretaceous of Hokkaido. *Ibid.* **23**, 303–366, pls. 43–61.
- and KANIE, Y. 1967. *Ainoceras*, a new heteromorph ammonoid genus from the Upper Cretaceous of Hokkaido. *Ibid.* **18**, 349–359, pls. 20 and 21.
- OKAMOTO, T. 1984. Theoretical morphology of *Nipponites* (a heteromorph ammonoid). *Kaseki (Fossils). Palaeont. Soc. Japan*, **36**, 37–51, pl. 1. [In Japanese.]
- 1988. Analysis of heteromorph ammonoids by differential geometry. *Palaeontology*, **31**, 35–52, pl. 7.
- RAUP, D. M. 1966. Geometric analysis of shell coiling: general problems. *J. Palaeont.* **40**, 1178–1190.
- 1967. Geometric analysis of shell coiling: coiling in ammonoids. *Ibid.* **41**, 43–65.
- and CHAMBERLAIN, J. A. 1967. Equations for volume and center of gravity in ammonoid shells. *Ibid.* 566–574.
- REYMENT, R. A. 1958. Some factors in the distribution of fossil cephalopods. *Stockh. Contr. Geol.* **1**, 97–184.
- 1973. Factors in the distribution of fossil cephalopods. Part 3: Experiments with exact models of certain shell types. *Bull. geol. Instn Univ. Uppsala*, ns, **4**, 7–41.
- SAUNDERS, W. B. and SHAPIRO, E. A. 1986. Calculation and simulation of ammonoid hydrostatics. *Paleobiology*, **12**, 64–79.
- TANABE, K. 1975. Functional morphology of *Otoscaphtes puerculus* (Jimbo), an Upper Cretaceous ammonite. *Trans. Proc. palaeont. Soc. Japan*, ns, **99**, 109–132, pls. 10 and 11.
- 1977. Functional evolution of *Otoscaphtes puerculus* (Jimbo) and *Scaphtes planus* (Yabe), Upper Cretaceous Ammonites. *Mem. Fac. Sci. Kyushu Univ. Ser. D, Geol.* **23**, 367–407, pls. 62–64.
- TRUEMAN, A. E. 1941. The ammonite body chamber, with special reference to the buoyancy and mode of life of the living ammonite. *Q. Jl geol. Soc. Lond.* **96**, 339–383.
- WARD, P. D. and WESTERMANN, G. E. G. 1977. First occurrence, systematics, and functional morphology of *Nipponites* (Cretaceous Lytoceratina) from the Americas. *J. Paleont.* **51**, 367–372, pl. 1.
- YABE, H. 1904. Cretaceous Cephalopoda from the Hokkaido. Part 2. *J. Coll. Sci. imp. Univ. Tokyo*, **20**, 1–45, pls. 1–6.

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